Visual Preferences of Imprinted Ducklings Are Altered by the Maternal Call

By: Timothy D. Johnston and Gilbert Gottlieb

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Abstract:

This study determined whether the visual characteristics of a familiar (imprinted) model or the auditory characteristics of the species maternal call are more important in determining the maternal preferences of visually imprinted ducklings. Domestic mallard (Peking) ducklings were visually imprinted to a stuffed model of a mallard duck during a 30-min following trial at 24 hr after hatching. Simultaneous choice tests between the familiar mallard model and an unfamiliar red-and-white-striped box at 48 hr and 72 hr confirmed the efficacy of the imprinting procedure: When both models were silent, subjects preferred to follow the familiar mallard model. However, when a recording of the mallard maternal assembly call was played from a speaker mounted inside the red box, subjects imprinted to the mallard preferred to follow the unfamiliar box rather than the familiar mallard model (Experiment 1). That preference was not due merely to the audiovisual stimulation provided by the box, since when a recording of intermittent tones was played from the mallard model, subjects imprinted to the mallard still preferred to follow the red box emitting the mallard call (Experiment 2). Playing only the tones from the red box disrupted the stability of the subjects' imprinted preferences between the first and second tests but did not produce a preference for the box (Experiment 3). These results show that the mallard maternal call is more important than visual experience with an inanimate model in determining the maternal preferences of visually imprinted Peking ducklings.

Article:

During the period following their exodus from the nest, the young of most precocial birds, such as ducks and chickens, remain in close contact with their mother (Collias & Collias, 1956; Lorenz, 1935). It is supposed that this close attachment results from a process of visual imprinting, which occurs during a brief early exposure of the young bird to its mother. A wealth of data from laboratory studies has been offered in sup-port of that supposition. Those data show that early exposure to almost any visually conspicuous object produces a strong, specific attachment to that object in young precocial birds (reviews by Bateson, 1966; Hess, 1973; Shapiro, 1980; Sluckin, 1973). Studies of imprinting have focused almost exclusively on the visual characteristics of the mother and the developmental processes whereby those characteristics become specifically attractive to the young. However, in nature, the mother also presents a significant auditory component, namely, a species-specific maternal assembly call, that is highly attractive to conspecific young (Gottlieb, 1971, 1974; Miller & Gottlieb, 1978). An important difference between the visual and auditory components of the mother's attractiveness to the young is in the role that experience plays in the development of that attractiveness. Whereas the visual characteristics of the mother only elicit preferential approach after the young have been exposed to them, the specific attractiveness of the maternal call is not de-pendent on previous exposure to it, as has been shown in a variety of precocial species (Gottlieb, 1971, 1981). (Prior auditory self- or sib-stimulation is required for the development of normal postnatal auditory responsiveness to the maternal call in both of the species studied thus far; Gottlieb, 1980a, 1980b.)

The role that the maternal call might play in determining the species-typical maternal preferences of visually experienced (imprinted) ducklings has received no attention in the literature. In discussions of imprinting, the function of the maternal call is generally limited to that of arousal, stimulating the naive bird to follow its

mother and hence become visually imprinted to her (e.g., Bateson, 1966; Fischer, 1966; Sluckin, 1973). However, the strong and highly specific preference of naive birds for the maternal call of their species suggests that, even in visually imprinted birds, the call may play an important role in determining maternal preferences. This possibility is further supported by recent experimental findings showing that ducklings visually imprinted to a natural stuffed model of a hen of their own species do not always prefer it to a model of a hen of a different species when the models differ only in their visual characteristics (Johnston & Gottlieb, 1981).

Thus, the present study was undertaken to determine whether the visual characteristics of a familiar (imprinted) model or the auditory characteristics of the maternal call are more important in determining the maternal preferences of visually imprinted ducklings. Domestic mallard (Peking) ducklings were visually imprinted to a replica of a mallard hen and then tested in a variety of choice situations involving the familiar visual replica and the mallard maternal call (to which they had riot previously been exposed).

General Method

Subjects

Incubator-reared Peking ducklings, a highly domesticated form of the mallard duck (Anas *platyrhynchos* L.), were used as subjects. Fertile, unincubated eggs were received weekly from a commercial supplier, washed, and stored in a refrigerator at 9 °C for 24 hr. The eggs were set in a Petersime Model IV incubator, which was maintained at 37.8 °C (±25 °C) and 65%-74% relative humidity, and were automatically turned every 6 hr. After 23 days of incubation, the eggs were transferred to hatching trays in the bottom oldie incubator. The hatching eggs were checked frequently. and the time at which each duckling hatched was re-corded to the nearest half hour. Hatched ducklings were placed in individual ventilated, opaque plastic boxes (10 cm^3) and transferred to a brooder, maintained at 31 °C, in which they could hear but not see other ducklings. No food or water was provided for the du-ration of the experiment.

The mean hatching success per weekly batch was 79% (*SD* = 9.1%, range = 60%-91%). Only those ducklings that hatched during Day 26 of incubation were used in the experiment.[1]

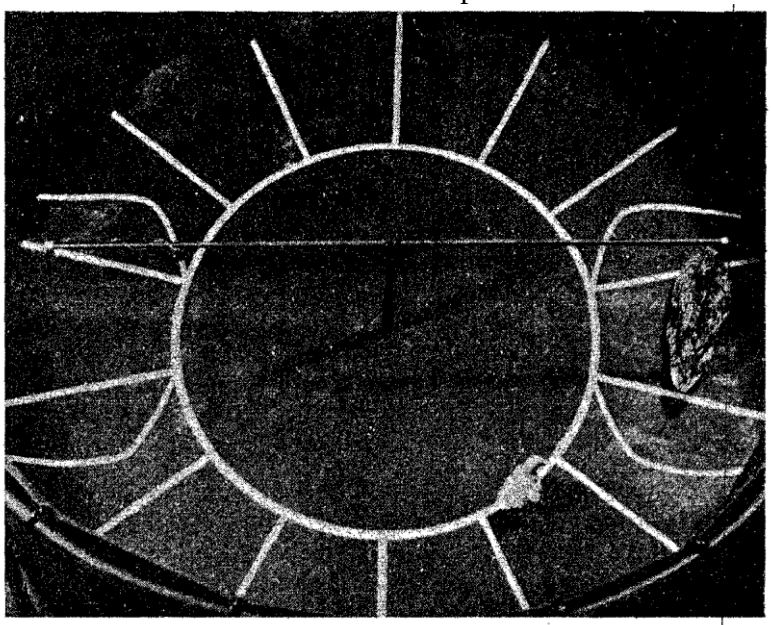

Figure 1. The circular testing arena as seen in the viewing mirror from the observer's station, showing a duckling approaching the mallard model during training. (During testing, the red box was suspended from the opposite end of the T-bar. The start point was the vertical white line at the top of the photograph, and the model is shown in the starting position. The models moved in a counterclockwise direction. The pattern of white lines on the floor of the apparatus facilitated scoring of following behavior during training and testing.)

Apparatus

Training and testing were conducted in a circular arena, 178 cm in diameter, surrounded by an 81-cm-high opaque black curtain which shielded the observer from the subject's view. Subjects were observed by means of

two angled mirrors suspended above the arena. The inside of the arena was painted flat black, with a pattern of white lines on the floor (see Figure 1) to facilitate the scoring of following behavior, as described below. A fine grit mixed with the paint provided a roughened surface to increase traction for the subjects. In the center of the arena was a vertical drive shaft which passed below the floor where it was connected to an electric motor geared to rotate the shaft at a constant speed of 1.2 rpm, The sound of the motor was not audible above the background noise in the testing room. Attached to the shaft above the floor of the arena was a T-shaped tubular suspension arm. The models were suspended from the ends of the crossarm and hung approximately 2 cm above the floor. When the motor was running, they moved around a circular path, 455 cm in diameter, at a constant speed of 9.1 cm/sec. The suspension bar and the hardware associated with the models were painted flat black.

The two models used in this study were a stuffed natural model of an adult female mallard and a red-and-white diagonally striped 15-cm^3 wooden box (see Figure 2). Each model was equipped with a hidden 9-cm-diameter loudspeaker. The speaker wires ran through the tubular suspension arm to a vacuum-sealed slip-ring assembly underneath the arena. The external (stationary) terminals on this assembly were connected to a Revox Model A77 stereo tape-recorder, which allowed calls to be broadcast from the models.

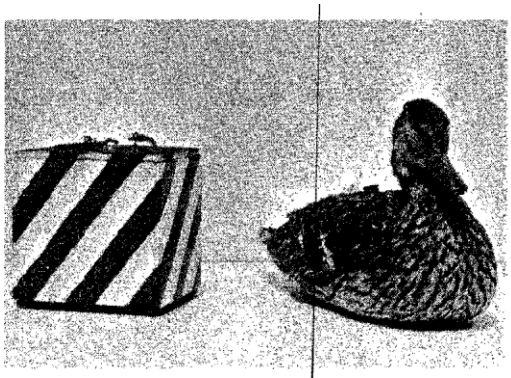

Figure 2. The two models used in the study. (Subjects were imprinted to the stuffed mallard model and then tested in a variety of choice situations involving these two models and the mallard maternal call.)

A tape-recorder and drive motor were operated by remote switches located at the observer's station. A system of foot-operated timeclocks was used to score the latency and duration of response to the models, as described in detail below. The testing room was maintained at approximately 20 °C throughout the study.

Table 1
Length of Incubation, Age at Training and Testing, and Training Performance of Each Experimental Group in Experiments 1–3

Group	*n*	No. of hatches	Length of incubation	Age at training[a] P.H.	Age at training[a] D.A.	% following in training	Training performance[b] Latency	Training performance[b] Duration	Age at first test[a] P.H.	Age at first test[a] D.A.	Age at second test[a] P.H.	Age at second test[a] D.A.
Experiment 1												
Group 1	29	3	26,16.9	24.6	27,17.4	72	298	918	48.5	28,17.4	72.5	29,17.5
			2.5	.8	2.2		39–344	467–1,295	1.0	2.2	1.4	1.8
Group 2	21	3	26,17.1	24.4	27,17.5	62	318	1,127	47.9	28,17.0	72.1	29,17.2
			3.1	.6	2.9		115–329	860–1,226	.9	2.7	1.2	2.3
Experiment 2												
Group 1	30	3	26,14.8	24.9	27,15.6	70	322	990	48.7	28,15.4	72.8	29,15.5
			6.2	.9	6.2		50–493	176–1,245	1.2	6.6	1.2	6.4
Group 2	25	4	26,14.4	24.5	27,14.8	68	340	804	48.5	28,14.9	72.8	29,15.1
			6.0	.8	6.0		318–642	235–1,040	.8	5.6	.9	5.6
Experiment 3												
One group	35	3	26,15.3	23.8	27,14.9	60	329	737	48.0	28,15.4	71.7	29,15.0
			4.9	.8	5.6		60–645	267–1,187	1.5	5.2	1.2	5.2

[a] Mean ages are given as posthatch (P.H.) in hours and developmental (D.A.) in days and hours (days,hours). Standard deviations beneath means are given in hours in both cases.
[b] Median and interquartile range are given in seconds for subjects that followed in training.

Procedure

Training. Each subject was given the same training, a single 30-min trial at 24 hr (± 3 hr) after hatching. The stuffed mallard model was suspended from one end of the T-bar and positioned 90° to the right of the start point (see Figure 1); the other end of the T-bar was always empty during training. At the beginning of the trial, the

subject was placed at the start point, and the tape-recorder and drive motor were turned on so that the calling model moved toward the subject. A calling rather than a silent model was used in training because pilot work showed that only about 10% of subjects would follow a silent model in our apparatus. The call used was a natural maternal assembly call of the wood duck (*Aix sponsa;* Miller & Gottlieb, 1976), which elicited following in 60%-70% of subjects (see Table 1). It consisted of a burst of 13 notes at a repetition rate of 6.9 notes/sec, played at a tape speed interval of 19 cm/sec with an interval of 3.5 sec between bursts. Prior to each training session, the call was adjusted to have a peak amplitude of 70 dB (B weighted scale, fast response), measured at the start point. The call was played only during the first minute of each 5-min period of the training trial (i.e., during the 1st, 6th, 11th, etc. min), for a total of 6 min during the 30-min trial.

The latency and duration of the subject's following response were scored as follows. A "following area" was defined, extending 12 cm to either side of the model and extending 30 cm behind its trailing edge. The latency of response was defined as the time from the start of the trial to the time when the subject first took three steps in the direction of movement of the model within the following area. The criterion of three steps was adopted to avoid scoring false starts. Once following began, its duration was recorded according to the following criteria: (a) More than half of the subject's body had to be within the following area, or, failing that, both feet had to be on the boundary of the area; (b) the subject had to be facing either toward the model or in the direction of movement of the model; and (c) the subject was allowed to pause within the following area, but a stationary subject was scored as following only if it had previously entered the following area by itself. This last criterion was adopted to avoid accumulating a following score for a motionless, properly oriented subject as the model moved past it, which would have overestimated the duration of following. The position of the following area with respect to the moving model could be accurately estimated by means of the grid lines on the floor (Figure 1). The sides of the area were defined by the inner circle and by the perimeter of the arena; the radial lines (spaced 30 cm apart at their midpoints) defined the successive positions of the trailing edge of the area. At the end of the training trial, the subject was removed from the arena, placed in its box, and returned to the brooder.

The durations of following during the calling and the silent periods of the trial were recorded separately. Those subjects that accumulated a total of at least 90 sec of following during the training trial were designated as followers. The percentage of birds following in each group, and their median latency and duration of following, are reported in Table 1. Occasionally, subjects fell on their backs or rode on top of the model; any subject that accumulated more than 4 min on its back or on top of the model (combined) was discarded, and such subjects are not included in the calculations of percentage following. Crippled subjects, which were unable to locomote properly, were similarly discarded. Less than 5% of subjects were discarded for these reasons.

Testing. Two test trials, each 10 min long, were given to each subject, whether or not it followed during training. One test was given at 48 hr (± 3 hr) and one at 72 hr (± 3 hr) after hatching (the exact mean age for each group is given in Table 1). The mallard and red-box models were suspended from opposite ends of the T-bar. At the beginning of the test trial, the subject was placed at the start point, with the two models 90° to its right and left, respectively. The starting position of the models was counterbalanced across subjects and alternated between trials for each subject. Two-auditory stimuli were used during testing, as described for each group below. One of them, referred to as the "call," was a natural mallard maternal assembly call, consisting of a burst of 9 notes at the normal repetition rate of 3.7 notes/sec. The other, referred to as the "tones," was a burst of eight 2-kHz tones, each 75 msec in duration, with a repetition rate of 2 notes/sec. The time between successive burst onsets was 6.3 sec in each case. In those tests in which both stimuli were used in testing (Experiment 2), they were played, one from each model, in a partially overlapping fashion: The last four notes of the tones overlapped the first five notes of the call. This procedure has been found to be most effective in producing a high rate of responding in simultaneous choice tests. Latency and duration of following each model were recorded as in training. Between the two test trials, the subject was placed in its box and returned to the brooder.

Data Analysis

Before performing the statistical analysis, any training-duration score of less than 90 sec and any testing-duration score of less than 30 sec were discarded and replaced with a score of zero, to avoid scoring accidental responses as the subject wandered around the arena. The corresponding latency scores were replaced with scores of 1,800 sec and 600 sec, respectively (the length of the respective trials). Subjects were assigned a duration score of zero and a latency score of 600 sec for the model(s) to which they did not respond. Two different measures of group preference in testing were obtained. Differences in the latency and duration scores of the subjects' responses to each model were evaluated by means of the Wilcoxon matched-pairs signed-ranks test. In addition, an individual preference was recorded for any subject that followed one model for more than twice as long as it followed the other. The significance of the preference shown by a group was evaluated by means of the binomial test. In summary, there were three measures of the birds' attraction to the test objects: latency of response, duration of response, and preference of each bird that responded. The first two are group measures, whereas the third offers a convenient summary of the performance of each bird in every experiment.

Experiment 1

Method

In order to determine the effect of the mallard maternal call on the preferences of visually imprinted ducklings for either the call or the visually familiar imprinting object (always the stuffed mallard model), 50 ducklings were trained with the mallard model and then assigned to one of two testing groups. Subjects in Group 1 (n = 29) were tested with the familiar silent mallard model versus an unfamiliar silent red box, to demonstrate the effectiveness of our imprinting procedure. The conventional expectation is that these subjects will show a preference for the familiar mallard model, and that expectation must be borne out if we are to determine the effect of the maternal call on the subjects' preference. To determine that effect, we tested subjects in Group 2 (n = 21) with the silent mallard model versus the red box emitting the mallard call.

Results and Discussion

Seventy-two percent of the subjects in Group 1, and 62% of those in Group 2, followed during training (Table 1).

The results of testing are shown in Tables 2 and 3. Subjects in Group 1 showed a significant preference for the familiar mallard model at both 48 hr ($p < .001$) and 72 hr ($p < .01$) after hatching (see Table 2). Analysis of the latency and duration scores supports that result. On both tests, subjects had shorter latencies ($p < .05$) and longer durations ($p < .01$) in their response to the mal-lard model than to the red box (Table 3.) The results of Group 2 were quite different, since at both 48 hr and 72 hr, subjects showed a significant preference for the calling red box rather than for the silent, but familiar, mallard ($p < .001$; Table 2). On both tests, subjects had shorter latencies and longer durations in their response to the red box than to the mallard model ($p < .001$ in all cases; Table 3).

Table 2
Preferences of Subjects in Simultaneous Choice Tests at 48 hr and 72 hr After Hatching (Experiment 1)

Group	*n*	Age (in hr)	*n* responding	Preference		
				Mallard	Red box	Both
Silent mallard vs. silent red box						
1	29	48	20	18**	2	0
		72	20	17*	3	0
Silent mallard vs. red box + call						
2	21	48	21	0	21**	0
		72	21	0	19**	2

Note. All subjects were tested at 48 hr (± 3 hr) and retested at 72 hr (± 3 hr) after hatching. See Table 1 for exac mean ages.
* $p < .01$; ** $p < .001$ (preferred model; binomial test).

Table 3
Latency and Duration of Response by Subjects in Simultaneous Choice Tests at 48 hr and 72 hr After Hatching (Experiment 1)

Group	*n*	Age (in hr)	*n* responding	Latency[a] (in sec)		Duration[a] (in sec)	
				Mallard	Red box	Mallard	Red box
			Silent mallard vs. silent red box				
1	29	48	20	178*	600	302***	0
				31–600	442–600	0–443	—
		72	20	141*	600	188**	0
				24–600	357–600	353–600	—
			Silent mallard vs. red box + call				
2	21	48	21	600	26***	0	342***
				—	14–46	—	176–537
		72	21	600	14***	0	500***
				—	9–19	—	232–554

Note. All subjects were tested at 48 hr (± 3 hr) and retested at 72 hr (± 3 hr) after hatching. See Table 1 for exact mean ages.
[a] Medians and interquartile ranges are given as summaries of group preformance. Measures of significance are based on the Wilcoxon signed-ranks test, which tests for differences between ranked scores, not between medians.
* $p < .05$; ** $p < .01$; *** $p < .001$ (shorter latency and longer duration).

The test results were not affected by the inclusion of birds that did not follow during training. In Group 1, only one nonfollower responded in testing (choosing the mallard model on both tests), and in Group 2, all the subjects that showed a preference, whether followers or nonfollowers, preferred the red box (see Table 2). Although fewer subjects in Group 1 than in Group 2 responded on each test (20/29 vs. 21/21), the proportions are not significantly different, $\chi^2(3) = 5.98$, $.2 > p > .1$.

The maternal call is evidently more potent in determining the preferences of imprinted ducklings than are the familiar visual characteristics of the imprinting object. It might be expected that the conflict between visual and auditory information in Group 2 would result in longer latencies to respond in that group, but, in fact, a comparison between those subjects that responded in each group showed that latencies to follow the red box in Group 2 were actually shorter than latencies to follow the mallard model in Group 1, at both 48 hr ($p < .05$) and 72 hr ($p < .01$; Mann-Whitney *U* test). Duration of response did not differ at either age. These results are further evidence for the potency of the maternal call in determining the choice behavior of ducklings in these test conditions.

Experiment 2

It is well known that audiovisual stimuli are, in general, more attractive to young ducklings than are visual stimuli alone (Boyd & Fabricius, 1965). Since Experiment 1 pitted a visual stimulus (the mallard model) against an audiovisual stimulus (the red box), it might be that the box was preferred simply because it was an audiovisual stimulus, rather than because of any specific properties of the mallard maternal call. To test this hypothesis, in Experiment 2 we added a second auditory stimulus, the tones described in General Method, to the test situation, so that both models presented audiovisual stimulation.

Method

Fifty-five ducklings were trained with the mallard model and then assigned to one of two testing groups. Subjects in Group 1 (n = 30) were tested with the familiar mallard model emitting the tones versus the unfamiliar red box emitting the mallard call. If the provision of auditory stimulation by both models is all that is required for the effects of visual imprinting to be shown, then the birds in Group 1 should prefer the familiar mallard model. If, on the other hand, the mallard call has specific attractive properties in this test situation, then the birds will show a preference for the unfamiliar red box; this would replicate the results of Experiment 1. To further examine the effectiveness of the call, we tested subjects in Group 2 (n = 25) with the mallard model emitting the mallard call versus the red box emitting the tones.

Results and Discussion

Seventy percent of the subjects in Group 1, and 68% of those in Group 2, followed during training (Table 1).

The results of this experiment are shown in Tables 4 and 5. Subjects in Group 1 showed a significant preference for the calling red box at both 48 hr and 72 hr ($p < .01$; Table 4). The analyses of the latency and duration scores support that result. On both tests, subjects had shorter latencies ($p < .001$) and longer durations ($p < .02$) of following the red box than the mallard model (Table 5). The results from Group 2 showed the opposite pattern. There was a significant preference for the calling mallard model at both 48 hr and 72 hr ($p < .001$; Table 4), and the subjects had shorter latencies and longer durations in their response to the mallard than to the red box on both tests ($p < .001$ in all cases; Table 5).

Table 4
Preferences of Subjects in Simultaneous Choice Tests at 48 hr and 72 hr After Hatching (Experiment 2)

Group	*n*	Age (in hr)	*n* responding	Preference		
				Mallard	Red box	Both
Mallard + tones vs. red box + call						
1	30	48	28	6	22*	0
		72	27	5	21*	1
Mallard + call vs. red box + tones						
2	25	48	22	21**	0	1
		72	22	22**	0	0

Note. All subjects were tested at 48 hr (± 3 hr) and retested at 72 hr (± 3 hr) after hatching. See Table 1 for exact mean ages.
* $p < .01$; ** $p < .001$ (preferred model; binomial test).

These results show that the preference for the calling red box in Experiment 1 was not due merely to the audiovisual stimulation that it provided. If that were the correct interpretation, we would expect the addition of an auditory component to the mallard model, as in Group 1 in this experiment, to eliminate the preference for the red box. In fact, that preference remained, and although a few more subjects chose the mallard emitting the tones in this experiment (Group 1) than chose the silent mallard in Experiment 1, Group 2, there was no significant difference between the preferences of these two groups on either test, $\chi^2(3) = 3.3$ and 2.4, $p > .3$ in both cases.

Table 5
Latency and Duration of Response by Subjects in Simultaneous Choice Tests at 48 hr and 72 hr After Hatching (Experiment 2)

Group	*n*	Age (in hr)	*n* respond-ing	Latency (in sec)		Duration (in sec)	
				Mallard	Red box	Mallard	Red box
Mallard + tones vs. red box + call							
1	30	48	28	600	53***	0	281*
				533–600	17–267	0–47	53–536
		72	27	600	22***	0	342**
				—	17–416	—	49–505
Mallard + call vs. red box + tones							
2	25	48	22	34***	600	434***	0
				17–65	—	210–557	—
		72	22	16***	600	496***	0
				9–53	—	283–572	—

Note. See footnotes to Table 3.
* $p < .02$; ** $p < .01$; *** $p < .001$ (shorter latency and longer duration; Wilcoxon test).

In Group 1 of the present experiment, four birds preferred the mallard model on both the 48-hr and 72-hr tests. It is of interest to ask whether those birds might have been sufficiently strongly imprinted to the mal-lard (as a

result of their experience during training) for visual imprinting to have overcome the attractive effects of the maternal call. That question cannot be answered by statistical analysis, since too few birds chose the mallard model in both tests. However, of those that did, two did not follow at all during training, and the training duration scores of the other two ranked 1st and 18th, respectively, out of 21 followers. Therefore, it is unlikely that those birds were especially strongly imprinted as a result of their behavior in training, and their performance seems more likely to be a chance result.

The preference shown by subjects in Group 2 for the mallard model is, of course, to be expected, since here there was no conflict between the preferred auditory and the familiar visual stimulation. However, such a conflict is present in Group 1, and we can examine its effect by comparing the latency and duration of response by subjects in the two groups. The most likely effect is that the audiovisual conflict in Group 1 might produce longer response latencies to the preferred model, in comparison with latencies in Group 2. It might also be that the conflict would reduce the persistence of following in Group 1, as measured by the duration scores. There is no difference between the two groups in latency of response to the preferred model at 48 hr, but at 72 hr, subjects in Group 2 (no conflict) had shorter latencies than did subjects in Group 1 (conflict; $p < .02$, Mann-Whitney U test). The duration of following was longer in Group 2 than in Group 1 at both 48 hr and 72 hr ($p < .01$).

That result suggests that when both models are vocal, a conflict between the attractive auditory stimulation presented by the mallard maternal call and the attractive visual stimulation presented by the familiar mallard model reduces the readiness of ducklings to choose to follow the maternal call. However, the presence of the conflict has no effect on the preference for the maternal call, since the preference for the calling box in Group 1 is not significantly different from the preference for the calling mallard in Group 2 at either 48 hr or 72 hr ($\chi^2(3) = 3.3$ and 2.9, respectively, $p > .3$ in both cases).

Experiment 3

The first two experiments in this study showed that the mallard maternal call has a potent effect on the maternal preferences of imprinted ducklings and that this effect is not due merely to the nonspecific auditory stimulation provided by the call. It would be interesting to know whether the sole presence of auditory stimulation other than the maternal call would have any effect on the subjects' preferences or whether the maternal call is unique in that respect.

Method

In this experiment we determined whether the tones alone, when emitted from the red box, would influence the preferences of subjects imprinted on the mallard model. Thirty-five subjects were trained with the mallard model and then tested with the silent mallard model versus the red box emitting the tones.

Table 6
Preferences of Subjects in Simultaneous Choice Tests at 48 hr and 72 hr After Hatching (Experiment 3)

Testing condition	n	Age (in hr)	n responding	Preference		
				Mallard	Red box	Both
Silent mallard vs. red box + tones	35	48	29	21*	7	1
		72	30	16	14	0

Note. All subjects were tested at 48 hr (± 3 hr) and retested at 72 hr (± 3 hr) after hatching. See Table 1 for exact mean ages.
* $p < .02$ (preferred model; binomial test).

Results and Discussion

Sixty percent of the subjects followed during training (Table 1).

The results of this experiment are presented in Tables 6 and 7. In contrast to the first two experiments, subjects in this experiment showed markedly different choice behavior in the first and second tests. At 48 hr, there was a significant preference for the silent mallard model ($p < .02$; Table 6), but at 72 hr, no preference for either

model was apparent. Analyses of the latency and du-ration scores support that result. At 48 hr, subjects had shorter latencies and longer durations in their response to the mallard model than to the red box *(p < .01;* Table 7), whereas at 72 hr, there was no difference in either latency or duration of response to the two models *(p* > .07 in both cases).

Table 7
Latency and Duration of Response by Subjects in Simultaneous Choice Tests at 48 hr and 72 hr After Hatching (Experiment 3)

Testing condition	*n*	Age (in hr)	*n* respond-ing	Latency (in sec)		Duration (in sec)	
				Mallard	Red box	Mallard	Red box
Silent mallard vs. red box + tones	35	48	29	126*	600	328*	0
				48–600	337–600	0–520	0–48
		72	30	46	600	33	0
				18–600	64–600	0–554	0–469

Note. See footnotes to Table 3.
* $p < .01$ (shorter latency and longer duration; Wilcoxon test).

General Discussion

Although the artificial stimulation pro-vided by the tones did not produce the dramatic shift in preference produced by the call, it did have a marked effect on the stability of the subjects' preferences. At 48 hr, the preference in Experiment 3 for the silent mallard was no different from that found in Experiment 1, Group 1, when no auditory stimulation was present, χ^2 (3) = .88, $p > .8$. That is to say, at 48 hr the tones had no influence on the subjects' imprinted preference. At 72 hr, however, the presence of the tones eliminated the imprinted preference for the mallard model. This result shows that auditory stimulation other than the maternal call can disrupt the stability of the maternal preferences of imprinted duck-lings.

Since only 21/35 subjects followed during training in this experiment, it might be that the results were caused by the 14 nonfollowers, whose preferences might have been more easily disrupted. That is not the case, however, because when the nonfollowers were excluded from the results, the same preference was found as when they were in- chided, at both 48 hr and 72 hr. Follower, showed a preference for the familiar mallard model at 48 hr *(p* < .02) and no preference for either model at 72 hr (Table 8).

Table 8
Preference of Those Subjects That Followed During Training in Experiment 3

Testing condition	Age (in hr)	*n*	Preference		
			Mallard	Red box	Both
Silent mallard vs. red box + tones	48	21	16*	4	1
	72	21	13	8	0

* $p < .02$ (preferred model; binomial test).

These experiments show that the species-typical maternal call is a far more important determinant of maternal preference in ducklings than is the 30-min visual imprinting experience used in this study. Gottlieb (1965, 1971) previously showed the maternal call to be a potent factor in eliciting following in maternally naive ducklings, and the present results are the first demonstration that this is also true for imprinted ducklings. Before discussing the implications of this result, let us briefly consider some alternative interpretations. It might be that the subjects in those groups that showed a preference for the unfamiliar red box over the familiar mallard model were les:, strongly imprinted to the mallard model because of differences in their experience during training. That possibility can be tested in two ways: by examining the pro-portions of followers and nonfollowers during training in the different groups and by examining the duration of following by those birds in each group that did follow. The proportions of followers and nonfollower,, did not differ among the groups, χ^2 (9) = 1.48, $p > .9$,

nor did the duration of following by those birds that did follow, Kruskal Wallis test, $H(4) = 4.93$, $p > .2$. Our results cannot, therefore, be attributed to differences in strength of imprinting resulting from differences in experience during training.

As noted in General Method, during training subjects were exposed to the stuffed mallard model emitting the wood duck maternal call, the call being employed to in-crease the amount of following during raining. That procedure raises the possibility that our results might be due to the effects of auditory imprinting to the wood duck call, effects that generalized to the acoustic features of the mallard call. Thus, we would have demonstrated a role for auditory imprinting in maternal choice, rather Alan a specific effect of the species-typical maternal call. The fact that naive Peking ducklings, which have never heard either call, strongly prefer the mallard call over the wood duck call (Gottlieb, 1971) argues against such an interpretation being correct, but more direct contrary evidence is also available. Gottlieb (1965) examined the effect of exposure to the wood duck call on the auditory preferences of Peking ducklings and found that after 20 min of active audio-visual following, subjects still showed a preference for the mallard over the wood duck call. Thus, it is safe to say that the 6 min of auditory exposure provided in the training session of this study are not sufficient to produce generalization from the acoustic features of the wood duck call to those of the mallard call. The effect of the mallard call on the preferences shown by the subjects during testing cannot, therefore, be attributed to their prior exposure to the wood duck call.

One final criticism of our results is that using a live rather than ail inanimate model might have resulted in stronger imprinting, so that the subject's visual preference would not have been altered by the call. The role 4 active maternal involvement in imprinting is an important problem that is yet to be thoroughly investigated (see Storey & Shapiro. 1979). However, it should be pointed out that our current understanding of the imprinting process is not based on studies with live models.

The finding that imprinted Peking ducklings prefer to follow the species-typical maternal call emanating from an unfamiliar object, rather than a familiar object that is either silent or emitting artificial auditory stimulation, has some important implications for our understanding of imprinting and the development of maternal preferences. There can be no question that in the 45 years since Lorenz's (1935, 1937) pioneering work on imprinting, the role of visual experience has been the dominant focus of research in the field. Lorenz (1937, p. 267-268) noted that auditory stimulation is often necessary to elicit following for the first time in young ducklings. Several more recent studies have shown that auditory, and especially audiovisual, stimulation is indeed more effective than visual stimulation alone in eliciting following during the first several days after hatching (e.g., Boyd & Fabricius, 1965; Gottlieb, 1963,1965,1971; Smith & Bird, 1963; see Bateson, 1966). Further-more, Gottlieb (1965,1971) showed that the mallard maternal call is uniquely attractive to naive (incubator-reared) mallard and Peking ducklings, being strongly preferred over the calls of other species in choice tests.

These studies all suggest that the maternal assembly call plays the role of an "innate perceptory pattern" (Lorenz, 1937, p. 266), guiding the following reaction to its "bio-logically proper object" (Lorenz, 1937), namely, the mother. Although young ducklings will follow almost any visually conspicuous moving object, the attraction exerted by the assembly call ensures that under normal circumstances the object that they actually follow will be their mother. Therefore, the relation between the attractiveness of the call and the process of visual imprinting has been interpreted as follows: The call arouses and directs the duckling's attention to its mother so that imprinting to her visual characteristics is ensured. The implication has been that once imprinting has occurred, the attractiveness of the mother's visual characteristics is what ensures that the duckling will continue to follow her.

However, the role that the call plays after imprinting to the mother has occurred has been ignored in studies of visual imprinting, and our results show that an important function for the call has been overlooked as a result. Not only does the call ensure a close attachment between the mother and her offspring before there has been any opportunity for imprinting to occur, but it also seems to bear the major responsibility for maintaining that

attachment after imprinting. Indeed, the role of visual imprinting in maintaining filial attachments seems to be of secondary importance to that of the maternal call, at least during the first 3 days of life.

In these experiments, we did not investigate the possible effects of postnatal auditory experience on the development of the ducklings' preferences; in fact, our experiments were designed to minimize any such effects. The important influence of the maternal call on the choice behavior of both naive and imprinted ducklings suggests that the call may also play a role in the development of social preferences, in addition to the relatively nonspecific role of arousing attention, noted above. It has already been demonstrated that in a number of precocial and semiprecocial species, postnatal auditory experience plays an important role in individual recognition of the mother's call by her young (e.g., Beer, 1970; Evans, 1980; Ramsay, 1951). Experiments are currently underway to examine further the developmental effects of postnatal exposure to the maternal call.

Comparative Considerations

The briefest excursion into the comparative literature on the audiovisual basis of early maternal attachments indicates that the auditory modality may be of rather widespread importance during early postnatal development. The present findings are not restricted to birds or to precocial species. Opossum young are summoned from the den by a peculiar clicking call given by their mother (Reynolds, 1952). Rat pups are attracted to conspecific vocalizations even after functional maturation of the visual system (Potash & Kelly, 1980). Human infants respond specifically to their own mother's voice when only 2 days old (DeCasper & Fifer, 1980), at which time their visual system is in a very immature state (Haynes, White, & Held, 1965).

Since studies of the relative importance of the visual and auditory modalities have not been conducted with the above species, we cannot, of course, determine whether the early auditory dominance continues even when visual learning becomes possible, as is the case in the present experiments. On the basis of our results, we suggest that such studies, using species-typical auditory and visual stimulation, would be a worthwhile comparative endeavor. As highly visual adult organisms, we may have allowed our own perceptual capabilities to unduly bias our ideas about the perceptual basis of early social attachments in our own and other species.

Notes:

1 The first 24-hr period *of* incubation is designated as Day 0, so that Day 26 begins at 26 day, 0 hr of incubation and ends at 26 day, 23 hr. The format day,hr (e.g., 26,17.5) is used to report lengths of incubation and developmental ages throughout this article. Mean length of incubation for each experimental group given in Table 1.

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